

## Allopatry and parapatry in hairstreak butterflies (Lycaenidae, Eumaeini) with uniform male sexual structures

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**Abstract.** An unusual characteristic of the *Electrostrymon guzanta* species complex is that its male primary and secondary sexual structures are uniform. Eumaeine taxonomy is often based on variation of these structures, and the taxonomy of this group is unresolved. Evolutionary changes in sexual structures are often hypothesized to promote reproductive isolation among closely related sympatric species, and the incidence of sympatry in this complex would be predicted to be low. To resolve the taxonomy and to assess the sympatry prediction, individuals of this species complex were partitioned into wing phenotypes based upon 21 qualitative characters, which were coded. We also measured 6 quantitative characters, which were analyzed with logistic regression. To determine the distinctiveness of phenotypes, the coded characters were analyzed with maximum parsimony because it provides the most efficient summary of the data. It also provides a hypothesis of character state evolution. Based on these results, the taxonomy of the *E. guzanta* species complex, including its nomenclature, was updated. *Electrostrymon thurman* Thompson & Robbins, **new species**, is named for high elevation individuals of the species complex from Costa Rica and western Panama (type locality). Chimeric holotypes of *Kisutam simplis* K. Johnson & Kroenlein, 1993 and *Angulopsis strymonotis* K. Johnson & Kroenlein, 1993 are restricted under ICZN article 73.1.5, and the latter name is synonymized with *Electrostrymon joya* (Dognin, 1895), **new synonym**. As predicted, the incidence of sympatry in the *E. guzanta* species complex is low. Three of the four species in the complex—*E. guzanta*, *E. thurman*, and *E. perisus*—are allopatric. The distribution of the fourth member of the species complex, *E. denarius*, overlaps that of *E. guzanta* and that of *E. thurman*, but it occurs at lower elevations (statistically significant). The theory of hybridization parapatry proposes areas of distributional overlap where there is reproductive interference. Data on reproductive interference are yet needed to determine whether this distributional overlap accords with the prediction of parapatry.

**Key words:** Calycopidina, *Electrostrymon*, hybridization parapatry, *guzanta*, *thurman*, secondary sexual structures.

## INTRODUCTION

The *Electrostrymon guzanta* (Schaus) species complex (Lepidoptera, Lycaenidae, Eumaeini, Calycopidina) is a primarily montane Neotropical monophyletic lineage (Figs. 1-21, 24-25) that is biologically unusual for eumaeines because males lack secondary structures on the wings and there are no evident interspecific differences in genitalic

morphology (Duarte & Robbins 2010). Male secondary sexual structures in insects are postulated to promote species recognition and to contribute to reproductive isolation among sympatric species (e.g., Löffstedt et al. 1991, Symonds & Elgar 2008). Further, interspecific genitalic differences among animals are usually hypothesized to result from sexual selection, which may allow females to select among conspecific males and to reject non-conspecific males (e.g., Eberhard 2010, Simmons 2014). According to this theory, then, we might hypothesize that a lineage with uniform male sexual structures, such as the *E. guzanta* species complex, would be composed of species that are allopatric or parapatric with each other.

The *E. guzanta* species complex possesses highly apomorphic genitalic structures so it is unambiguous which individuals belong to the complex (Duarte & Robbins 2010), but the species level classification of the complex is unresolved. For example, seven specific names have been proposed for this lineage,

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but it is unclear which, if any, apply to individuals from higher elevations in Costa Rica and Panama (Robbins 2004, Robbins et al. 2012a). Since genitalia and male secondary sexual structures cannot be used to distinguish species in this complex, it was suggested that an analysis of wing pattern variation might provide evidence on which to base a species level classification (Robbins et al. 2012a).

In the first part of the paper, we describe and code geographically variable qualitative and quantitative wing pattern traits in the *E. guzanta* species complex. For the qualitative characters, we looked for discrete states that partition the complex into phenotypes. For the variable quantitative characters, we analyzed them with logistic regression. To determine the distinctiveness of the phenotypes, we analyzed the characters with maximum parsimony because it is the most efficient summary of interspecific differences (Farris 1979), regardless of the phylogeny, and because it represents a widely used phylogenetic estimator for morphological characters. These results are the foundation for a species level taxonomy for the *E. guzanta* complex, including the description of a new species. In the second part of the paper, we ask if the species that we recognize are sympatric. In most cases, the answer is simple and straightforward. In one comparison, we use the theory of hybridization parapatry (Key 1981, Bull 1991, Pettengill & Moeller 2012, Werner et al. 2014, Bournez et al. 2015) to interpret the results for those species that occur at overlapping elevations in the same geographic area.

## MATERIALS AND METHODS

The results in this paper are based primarily upon 352 museum specimens belonging to the *E. guzanta* species complex. The specimens cited in this study are deposited in the following collections, with abbreviations and museum names from Evenhuis (2015) when available.

**BMNH** — The Natural History Museum [formerly British Museum (Natural History), London, UK.

**CUIC** — Cornell University, Ithaca, New York, USA.

**ICN** — Instituto de Ciencias Naturales de la Universidad Nacional, Universidad Nacional de Colombia, Bogotá, Colombia.

**MZFC** — Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F., Mexico.

**PMT** — Private Collection of Paul M. Thompson, Chantilly, Virginia, USA.

**USNM** — National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

The following abbreviations are used: FW—forewing; HW—hindwing; D—dorsal; V—ventral. Following Klotz (1951) and Ehrlich and Ehrlich (1961), the “limbal” part of the wing refers to the area of the ventral wings between the postmedian and submarginal lines. Wing venation follows Comstock (1918). The species names used were identified from their original descriptions and/or from examination of type specimens in the BMNH or USNM. All statistical tests were done with commercially available SAS JMP software.

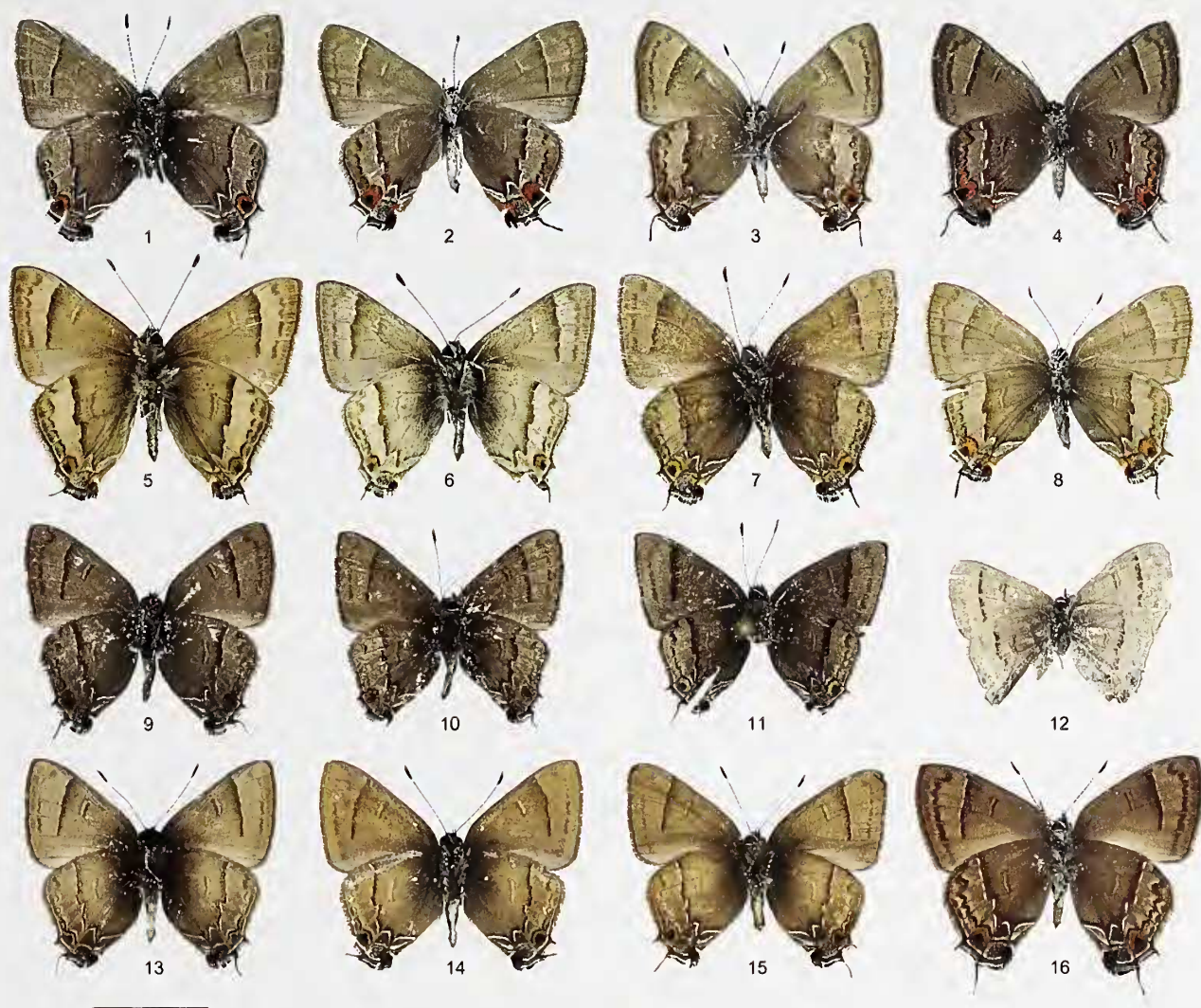
The preliminary classification of the *E. guzanta* species complex in Robbins (2004) was used as an initial guide in finding variable traits that formed discrete states, which were then used to characterize phenotypes. We specifically looked for characters that might modify the preliminary classification as well as for variable characters that would indicate the affinity of the high elevation specimens from Panama and Costa Rica.

We used digital Vernier calipers to measure quantitative traits in each sex that appeared to vary among phenotypes. It was our original intention to analyze the quantitative data using discriminant analysis, which assumes that variates are normally distributed. However, Shapiro-Wilk and Lilliefors tests showed significant departure from normality in about 20% of the comparisons. For this reason, we analyzed measurements between taxa using logistic regression (Hosmer et al. 2013), which does not assume normality.

We used multinomial logistic regression to determine the degree to which different quantitative characteristics differentiate groups of taxa. Although oversimplified, a nearly vertical logistic regression line indicates that a character distinguishes two groups of taxa, while an inclined line does not. For groups of taxa that separated via multinomial logistic regression, we performed binary logistic regression to confirm the differentiation. Using the binary model, we considered a character to be distinguishing if the value of McFadden’s pseudo- $R^2$ ,  $R^2(U)$ , produced by the logistic regression model exceeded 0.995 (Fig. 22).

To determine differences between phenotypes, we used maximum parsimony optimization in TNT and WinClada software (Nixon 2002, Goloboff et al. 2008). As noted, parsimony optimization provides the most efficient mathematical summary of the information in a data matrix (Farris 1979). Further, the optimized changes in character state are hypothesized evolutionary changes. We used *Electrostrymon constantinoi* (K. Johnson & Kroenlein) as an outgroup because it was the sister to the *E. guzanta* species complex in a previous phylogenetic analysis (Duarte & Robbins 2010).

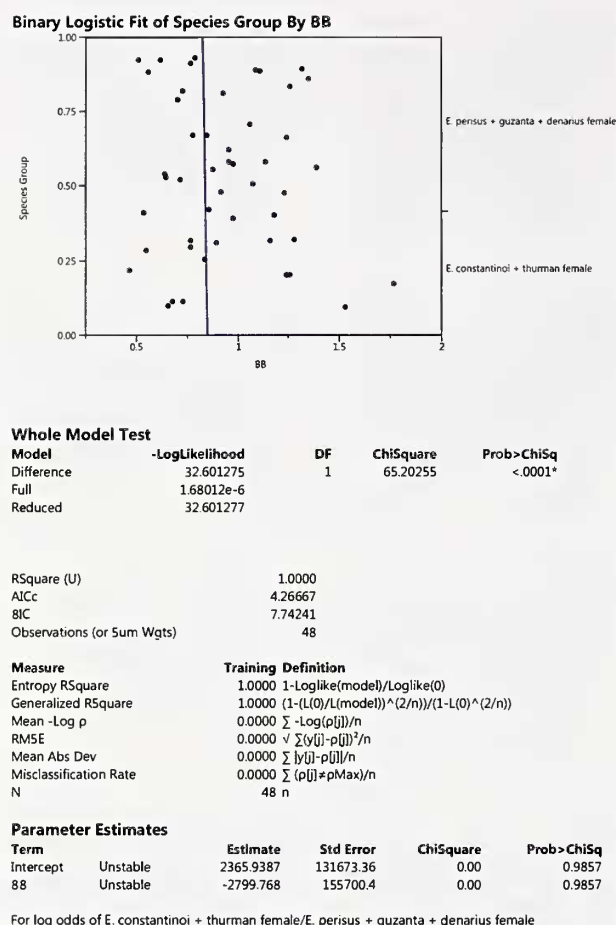




**Figures 1-16.** Ventral wing pattern variation in the *E. guzanta* species complex. 1. *E. guzanta* male (Mexico). 2. *E. guzanta* male (Mexico). 3. *E. guzanta* male (Nicaragua). 4. *E. guzanta* female (Nicaragua). 5. *E. thurman* male (Panama). 6. *E. thurman* male (Panama). 7. *E. thurman* male (Panama). 8. *E. thurman* female (Panama). 9. *E. perisus* male (Colombia). 10. *E. perisus* male (Colombia). 11. *E. perisus* male (Colombia). 12. *E. perisus* female (Colombia). 13. *E. denarius* male (Nicaragua). 14. *E. denarius* male (Panama). 15. *E. denarius* male (Panama). 16. *E. denarius* female (Panama). Scale 1 cm.



**Figures 17-21.** Dorsal wing pattern variation in *E. denarius*. 17. Male (Panama). 18. Male (Panama). 19. Male (Mexico). 20. Male (Nicaragua, El Crucero/Las Nubes). 21. Female (Panama).



**Figure 22.** Binary logistic regression analysis of Character 26 (Table 2) differentiating females of *E. constantinoi* and *E. thurman* from the others.

Based on the results of the wing pattern analyses, we updated the taxonomy and nomenclature of the *E. guzanta* species complex, including the description of a new species according to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). As part of the species description, genitalic morphology follows Klots (1970) as modified for the Eumaeini (Robbins 1991). Other morphological terms follow Snodgrass (1935). Nomenclature is updated and summarized in a list. Labels on the holotype are given verbatim with comments in brackets. Months are reported by their first three letters in English (other than the holotype label). Finally, we note that *E. guzanta* has been recorded from the United States (Texas) (Warren et al. 2004) on the basis of one female specimen and on various adult images (North American Butterfly Association, <http://www.naba.org/chapters/nabast/guzanta.html>, Butterflies of America, <http://www.butterfliesofamerica.com/L/>

Lycaenidae.htm, accessed 19 May 2015). We address the identification of Texan specimens elsewhere (Thompson & Robbins, in prep.).

Allopatry of species that occur in different countries is a straightforward determination. To assess the hypothesis of elevational parapatry in the *E. guzanta* species complex, we restricted the “elevation study series” to those specimens in which elevation was specifically noted on the data label. We did not include data if elevation was omitted or was given as a range. We plotted the number of localities where each species had been found for each elevation and country. Mexico was restricted because of its large size to the south-central part of the country bounded on the north by the trans-volcanic mountain range (about 19°N latitude) and on the east by the Isthmus of Tehuantepec (about 95°W longitude). This area included the states of Michoacán, Morelos, Guerrero, Oaxaca (north of the Isthmus of Tehuantepec), and Veracruz (south of Orizaba). We omitted Nicaraguan specimens. Virtually all Nicaraguan museum specimens of Eumaeini are deposited in BMNH or USNM, but those in BMNH lack elevation data and those in USNM are given as a range of elevations for localities above 1,000 m (Robbins et al. 2012a). We used the nonparametric Wilcoxon (Mann-Whitney) test for independent samples to determine whether there were significant differences in elevation localities for each species in a country because there was no a priori reason to expect the frequency of elevation localities to be normally distributed.

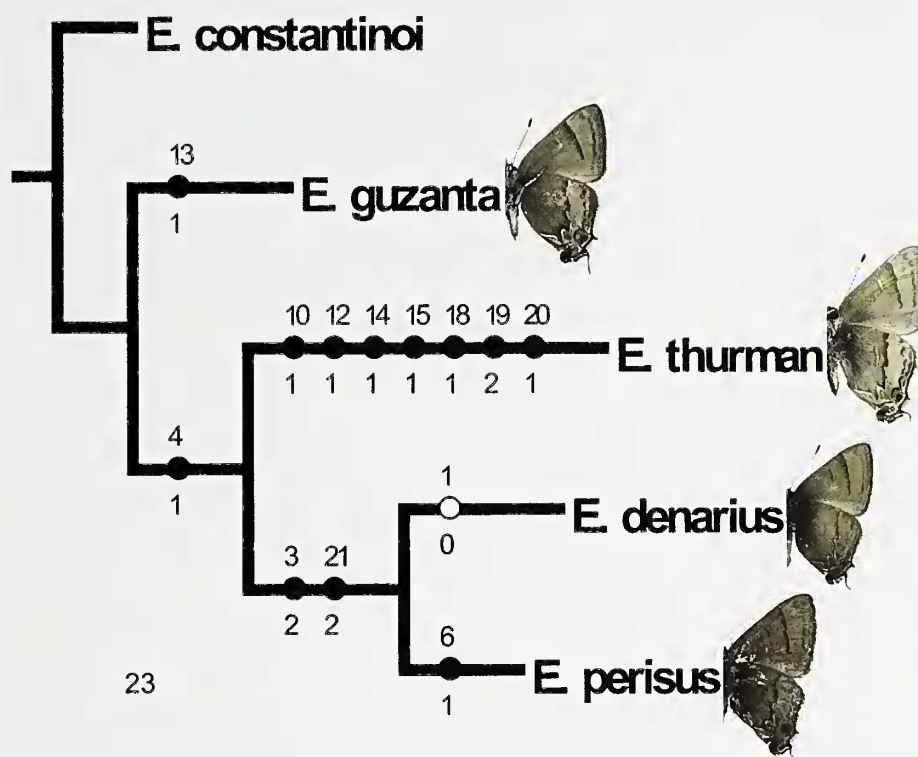
## RESULTS AND DISCUSSION

### Wing Pattern and Genitalic Variation

Representative ventral wing pattern variation in the *E. guzanta* species complex is illustrated (Figs. 1-16). The dorsal wings of both sexes of *E. guzanta*, *E. thurman*, and *E. perisus* are brown with an orange anal lobe (cf. Figs. 24-25). In contrast, *E. denarius* has orange scaling dorsally, but the amount of orange scaling is sexually dimorphic and geographically variable (Figs. 17-21).

We identified 21 variable wing pattern characters in the *E. guzanta* species complex that had discrete, qualitatively different states (Table 1). Minor variation within each state is noted (Table 1). We measured 6 quantitative characters. One of these distinguished female groupings based upon logistic regression (Character 26 in Table 2, Fig. 22). None of the quantitative characters differentiated male groupings in the logistics regression analysis. However, the mean, standard deviation, and range of





**Figure 23.** Most parsimonious tree for *E. guzanta* species complex with unambiguous character state changes (CI = 91, RI = 57). Hollow circles represent homoplastic changes.

the quantitative characters in Table 2 may be useful for distinguishing phenotypes when measurements are not in an area of overlap. One ratio in the logistic regression differentiated female groupings in the same way as Character 26 (Table 2), but was not independent of this character.

We assigned individuals to one of four wing pattern phenotypes differentiated by the character states in Tables 1 and 2. The taxonomy and nomenclature section below provides the rationale for the names that we apply to these phenotypes. These phenotypes differ from the previous taxonomy in that (1) high elevation specimens from Costa Rica and Panama represent a phenetically distinct taxon that is also phylogenetically distinct (Fig. 23) and (2) there is geographic variation within *E. denarius* (Figs. 17-20). These discrepancies from the previous classification are addressed in the taxonomy and nomenclature section.

We coded the qualitative characters (Table 1). Based on these data, there was one most parsimonious 33-step equal weight tree (Fig. 23). Further, each implied weight most parsimonious tree with values for the parameter K=1, 10 100, 1000 resulted in one tree,

also with the same topology as the most parsimonious equal weight tree. Unambiguous optimization shows where distinguishing character states are hypothesized to have evolved (Fig. 23).

The male and female genitalia of *E. thurman* are illustrated (Figs. 26, 27). We found no evident variation in a comparison of 13 male genitalic preparations among the four wing pattern phenotypes. There was minor intraspecific variation in the shape of the valvae and in the size of the more posterior cornutus, but none of the wing phenotypes could be distinguished by these structures. We also compared six female genitalic preparations. The female genitalia are small and relatively non-descript, and the signa are less conspicuous than they appear in Fig. 27.

## TAXONOMY AND NOMENCLATURE

### Taxonomic history

**Generic placement.** The current members of the *E. guzanta* species complex were placed in the adjoining *Thecla endymion* (Fabricius) and *T. cecrops*

**Table 1.** Qualitative wing pattern characters for distinguishing species in the *E. denarius* species complex. The outgroup is *E. constantinoi*. The number to the right of each character description is its coded state for the parsimony analysis. The term "limbal area" denotes the wing area that lies between the postmedian and submarginal lines.

Char #	Character	<i>E. constantinoi</i>	<i>E. guzanta</i>	<i>E. thurman</i>	<i>E. denarius</i>	<i>E. perisus</i>
1	Male dorsal wing color	Brown; with orange suffusion on both wings	0 Brown	1 Brown	1 Brown; with orange suffusion on both wings	0 Brown 1
2	Female dorsal wing color	Brown; with sky-blue suffusion on HW	0 Brown; with faint orange suffusion on both wings	1 Brown	2 Brown; with faint orange suffusion on both wings	1 Brown 2
3	Edges of DHW anal lobe	Brown on outer & inner margins; and females on vein CuA <sub>2</sub>	0 Little or no dark brown basally	1 Little or no dark brown basally	1 Entirely surrounded by dark brown	2 Entirely surrounded by dark brown
4	Male DHW submarginal white scaling	Anal lobe to Cu2	0 Anal lobe to Cu2	0 White spot adjacent to anal lobe	1 White spot adjacent to anal lobe	1 White spot adjacent to anal lobe
5	Female DHW submarginal white scaling	Anal lobe to M1	0 Anal lobe to Cu2	1 White spot adjacent to anal lobe	2 White spot adjacent to anal lobe	2 White spot adjacent to anal lobe
6	Width of basal part of VFW postmedian line	Thin	0 Thin	0 Thin	0 Thin	1 Broad
7	Color of basal part of VFW postmedian line	Bright orange	0 Brown (or brown with hints of dull orange)	1 Brown	1 Brown	1 Brown
8	Middle part of VFW postmedian line	Thin	0 Thin	0 Absent	1 Wide	2 Wide
9	Faintness of distal (white) part of VFW postmedian line	Not faint	0 Faint	1 Very faint	1 Very faint	1 None or very faint
10	Faintness of basal part of VHW postmedian line	Not faint	0 Not faint	0 Faint	1 Not faint	0 Not faint
11	Color of basal part of VHW postmedian line	Bright orange	0 Orangish brown	1 Orangish brown	1 Orangish brown	1 Orangish brown
12	Color of middle part of VHW postmedian line	Black	0 Black	0 Brown	1 Black	0 Black
13	Width of distal part of VHW postmedian line	Thin	0 Broad	1 Thin	0 Thin	0 Thin
14	Color of distal part of VHW postmedian line	White	0 White	0 Cream	1 White	0 White



Table 1. Cont.

Char #	Character	<i>E. constantinoi</i>	<i>E. guzanta</i>	<i>E. thurman</i>	<i>E. denarius</i>	<i>E. perisus</i>
15	Color of limbal area of VFW and VHW	Medium brown; (female slightly lighter and male same color as discal area)	Medium brown (slightly lighter than discal area)	Very light, beige to pale brown (much lighter than discal area)	Medium brown (slightly lighter or same color as discal area)	Medium brown (slightly lighter than discal area)
16	Color of VHW cubital spot	Orange with thin yellow suffusion	Red-orange to orange	Orange to yellow-orange	Yellow to yellow-orange	Mostly brown, rarely yellowish-brown
17	Size of VHW cubital spot	Medium	Large	Small	Small	Small
18	Color of basal portion of area between distal border of VHW cubital spot and base of fringe	Brown	Brown	Cream	Brown	Brown
19	Width of distal portion of area between distal border of VHW cubital spot and base of fringe	Thick	Thin	None	Thin	Thin
20	Orange ring surrounding VHW anal lobe black spot	No	No	Yes	No	No
21	VHW submarginal orange markings	Orange spot in cell 2A intrudes broadly into but not across cell Cu2; cell M3 has hints of orange	Orange spot in cell 2A extends at least halfway across lunule in cell Cu2; Orange line from vein Cu2 to vein M3 or beyond	Orange spot in cell 2A extends at least halfway across lunule in cell Cu2; Orange line from vein Cu2 to vein M3 or beyond	None	None

**Table 2.** Quantitative wing pattern characters for distinguishing species in the *E. denarius* species complex. The outgroup is *E. constantinoi*.  $\bar{X}$  = sample mean; S = sample standard deviation, R = sample range (minimum, maximum); N = sample size.

Char #	Character	<i>E. constantinoi</i>	<i>E. guzanta</i>	<i>E. thurman</i>	<i>E. denarius</i>	<i>E. perisus</i>
22	Male FW length (mm)	$\bar{X}$ = 12.38	$\bar{X}$ = 13.50	$\bar{X}$ = 12.52	$\bar{X}$ = 11.22	$\bar{X}$ = 12.27
		S = 0.106	S = 0.920	S = 0.717	S = 0.687	S = 0.770
		R = 12.30, 12.45	R = 11.72, 14.83	R = 11.42, 13.88	R = 9.51, 12.29	R = 11.24, 13.31
		N = 2	N = 18	N = 16	N = 16	N = 8
23	Female FW length (mm)	$\bar{X}$ = 12.23	$\bar{X}$ = 12.79	$\bar{X}$ = 13.03	$\bar{X}$ = 12.38	$\bar{X}$ = 11.02
		S = 0.443	S = 1.025	S = .744	S = 0.833	S = 0.770
		R = 11.94, 12.74	R = 11.18, 14.74	R = 11.76, 14.35	R = 11.18, 13.48	R = 11.02, 13.31
		N = 3	N = 21	N = 17	N = 6	N = 1
24	Male height of VHW cubital spot central black & brown areas (mm)	$\bar{X}$ = 0.49	$\bar{X}$ = 1.09	$\bar{X}$ = 0.72	$\bar{X}$ = 0.83	$\bar{X}$ = 1.02
		S = 0.035	S = 0.164	S = 0.111	S = 0.095	S = 0.084
		R = 0.46, 0.51	R = 0.89, 1.45	R = 0.55, 0.88	R = 0.68, 1.03	R = 0.94, 1.13
		N = 2	N = 19	N = 15	N = 16	N = 7
25	Male height of VHW cubital spot & distal white border (mm)	$\bar{X}$ = 1.75	$\bar{X}$ = 2.01	$\bar{X}$ = 1.70	$\bar{X}$ = 1.30	$\bar{X}$ = 1.61
		S = 0.190	S = 0.192	S = 0.166	S = 0.130	S = 0.152
		R = 1.62, 1.89	R = 1.69, 2.26	R = 1.50, 2.19	R = 1.08, 1.52	R = 1.35, 1.77
		N = 2	N = 19	N = 15	N = 16	N = 7
26	Female height of VHW cubital spot central black & brown areas (mm)	$\bar{X}$ = 0.51	$\bar{X}$ = 1.16	$\bar{X}$ = 0.70	$\bar{X}$ = 1.18	$\bar{X}$ = 0.86
		S = 0.045	S = 0.207	S = 0.084	S = 0.238	S = 0.152
		R = 0.47, 0.56	R = 0.90, 1.77	R = 0.54, 0.84	R = 0.88, 1.53	R = 0.86, 1.77
		N = 3	N = 20	N = 17	N = 6	N = 1
27	Female height of VHW cubital spot & distal white border (mm)	$\bar{X}$ = 1.86	$\bar{X}$ = 1.99	$\bar{X}$ = 1.73	$\bar{X}$ = 2.02	$\bar{X}$ = 1.34
		S = 0.098	S = 0.229	S = 0.210	S = 0.278	S = 0.152
		R = 1.75, 1.92	R = 1.58, 2.43	R = 1.37, 2.21	R = 1.65, 2.49	R = 1.34, 2.49
		N = 3	N = 20	N = 17	N = 6	N = 1

**Table 3.** Statistical comparison of the elevations at which different taxa are recorded.

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value	Hodges-Lehmann	Lower CL	Upper CL
<i>E. thurman</i> Panama	<i>E. perisus</i> Colombia	-2.25	1.920286	-1.1717	0.2413	-350	.	.
<i>E. thurman</i> Panama	<i>E. guzanta</i> Mexico South	-3.0441	3.21746	-0.94612	0.3441	-175	-600	270
<i>E. perisus</i> Colombia	<i>E. guzanta</i> Mexico South	1.1765	3.702006	0.31779	0.7506	100	-450	770
<i>E. denarius</i> Panama	<i>E. denarius</i> Mexico South	-3.6825	2.393996	-1.53824	0.124	-160	-490	50
<i>E. denarius</i> Panama	<i>E. denarius</i> Costa Rica	-1.625	2.340267	-0.69437	0.4875	-135	-550	1130
<i>E. denarius</i> Mexico South	<i>E. denarius</i> Costa Rica	0	2.078805	0	1	15	-450	1300
<i>E. guzanta</i> Mexico South	<i>E. denarius</i> Mexico South	9.479	3.174156	2.9863	0.0028 *	650	250	1000
<i>E. thurman</i> Panama	<i>E. denarius</i> Panama & Costa Rica	8.647436	2.77735	3.113556	0.0018 *	600	200	1080



(Fabricius) species groups (Draudt 1919-1920: 795-797) until Johnson and Kroenlein (1993b: 3-5) named *Pendantus*, noting the distinctive shape of the male genitalia labides in lateral aspect (Fig. 26). In a checklist *Pendantus* was preliminarily synonymized with *Ziegleria* K. Johnson (Robbins 2004) based on the lack of a sclerotized ridge on the lateral edge of the female 8<sup>th</sup> abdominal tergum. However, a subsequent phylogenetic analysis found that *Pendantus* is a lineage nested within *Electrostrymon* Clench, not within *Ziegleria*, which remains a phylogenetically valid genus (Duarte & Robbins 2010).

***Electrostrymon guzanta* species complex.** Highly autapomorphic male and female genitalic structures characterize the *E. guzanta* species complex (Duarte & Robbins 2010), especially the “rectangular” shape of the male genitalia labides (first noted by Johnson & Kroenlein 1993b). However, Johnson and Kroenlein (1993b) included in *Pendantus* some species, such as *Arzecla sethon* (Godman & Salvin), which lack the male genitalia labides synapomorphy. Conversely, they described new species in other genera that possess the synapomorphy (see nomenclatural list below for specifics). A possible explanation for these seemingly incongruent results is that Johnson and coworkers routinely illustrated adults and genitalia that are not from the same individual, this result being most evident when the sex of the adult and the genitalia were different (cf. Robbins & Lamas 2002 and the results below).

### ***Electrostrymon thurman* Thompson & Robbins new species**

(Figs. 5-8, 24-29)

**ZooBank LSID:** urn:lsid:zoobank.org:pub:3F44721B-329C-4D14-BD8B-E8D11E8CBF1C

**Diagnosis and Description.** *Electrostrymon thurman* is placed in *Electrostrymon* following Duarte and Robbins (2010) because the female genitalia corpus bursae is less than 2 mm long, it possesses vestigial “fan-shaped” signa (Fig. 27), and the male genitalia gnathos lack teeth (Fig. 26).

*Electrostrymon thurman* is placed in the *E. guzanta* species complex because its male and female genitalia (Figs. 26-27) are indistinguishable from those of *E. guzanta*. Specifically, the unique rectangular posterior shape of the labides (Fig. 26) is a synapomorphy for the *E. guzanta* species complex (Duarte & Robbins 2010).

Analysis of wing pattern variation (including adult size) shows that *E. thurman* is unambiguously distinguished from the other taxa in the *E. guzanta* species complex by Characters 10, 12, 14, 15, 18, 19, and 20 (Table 1, Fig. 23). It is additionally distinguished from *E. denarius* + *E. perisus* by characters 3 and 21 and from *E. guzanta* by characters 4 and 13.

**Holotype** ♂ (Fig. 24). [off-white label with black ink handwriting] Panama: Chiriquí/Volcán Barú 1800 m/II[Feb]-8 [19]76/G. B. Small. [red label with black printing] Holotype/*Electrostrymon thurman*/Thompson & Robbins. Deposited USNM.

**Paratypes** (27♂ & 8♀, deposited USNM unless noted otherwise). Costa Rica. 2♀ Mount [Volcán] Poás, May. Panamá, Chiriquí. 1♂, 1♀ Cerro Punta, 5400 ft, 30 Jun 1965, 2 Jul 1965. 3♂, 1♀ Cerro Totuma, 6350 ft, 21 Feb 2012 (PMT). Volcán Barú. 1♀ 5400 ft, 18 Aug 1975; 3♂, 1♀ 1700 m, 22 Feb 1977, 23 Feb 1977, 19 Mar 1976, 9 Apr 1979; 11♂ & 1♀ 1800 m, 1-22 Feb 1976; 8♂ 1800 m, 9 Apr 1979; 1♂ 1800-2000 m, 12 Apr 1979; 1♀ 2300 m, 12 Apr 1979.

**Etymology.** This species is named for Albert Thurman, in recognition of his four decades of collecting and studying Panamanian Lepidoptera, and of encouraging others to do the same. The name is a noun in apposition.

**Female.** The sexes of *E. thurman* are associated because they occur at the same localities and have wing patterns that are exceedingly similar. It is sometimes difficult to determine the sex of an individual solely by wing pattern.

**Variation.** The ventral wing ground color varies from tan to gray to charcoal, as illustrated (Figs. 5-7).

**Superficially Similar Species.** *Electrostrymon thurman* is most likely to be confused with sympatric individuals of *A. sethon*, but is distinguished by both male and female genitalic characters, as outlined in Duarte and Robbins (2010).

**Distribution** (Fig. 28). Costa Rica and western Panama.

**Habitat.** *Electrostrymon thurman* inhabits the Tropical Lower Montane Rain Forest life zone (Holdridge 1967) and is recorded from 1,650-2,300 m elevation (Fig. 29).

**Behavior.** Males displaying territorial behavior were collected along a mountain road (1,800-2,000 m) on the eastern slopes of Volcán Barú, Chiriquí. Nine males were collected from 10:00-11:30 hours on 9 Apr 1979, and two more from 13:00-14:00 hours on 12 Apr 1979 (vouchers in USNM). In Feb 2012, adult males and females were observed nectaring at flowering trees at the edge of a ridgetop pasture in lower montane forest in the early afternoon on a sunny and windy day (Fig. 29).

**Caterpillar food “plant”.** Most caterpillar food “plant” records for the Calycopidina, including *Electrostrymon*, are plant detritus (Duarte & Robbins 2010, Robbins et al. 2010). We presume that caterpillars of *E. thurman* also eat plant detritus, at least facultatively.

**Recognition as a distinct species.** The data in Tables 1 and 2 show that *E. thurman* is phenotypically distinct. The most parsimonious cladogram (Fig. 23) suggests that it is monophyletic and phylogenetically distinct. The traits that it shares with the allopatric *E. guzanta* appear to be symplesiomorphies. The distribution of *E. thurman* overlaps that of *E. denarius*, which is part of its sister lineage. All previously proposed specific names refer to other phenotypes. Treating *E. thurman* as a distinct new species is in accord with these results.

**Remarks.** The distribution and elevation of *E. thurman* and *Kisutam rosemary* Thompson & Robbins are nearly identical (cf. Thompson & Robbins 2015), as far as is known. Wherever one occurs, the other might be expected. However, the two species have distinctly different biogeographical relationships. Whereas the sister species of *E. thurman* occurs in the South American mountains and Central American lowlands, the sister of *K. rosemary* is endemic to the mountains of northern Central America. They also differ in that *E. thurman* appears to be a common species while *K. rosemary* is uncommon, at least judging by the number of specimens in museum collections.

### **Geographical variation of *E. denarius***

Individuals of *E. denarius* from El Crucero/Las Nubes, Managua, Nicaragua (approximately 11°55'16"N, 86°16'32"S) possess more dorsal orange scaling on both wings (Fig. 20) than others of this



**Figures 24-25.** Types of *E. thurman*, dorsal surface on left. 24. Male holotype (Panama). 25. Female paratype (Panama). Scale 1 cm.

species (Figs. 17-19), including the Nicaraguan type of *Thecla calena* Hewitson. El Crucero/Las Nubes is subtropical humid forest at 700–900 m elevation that is located from 18 km SSW to 25 km S of the city of Managua (Robbins et al. 2012a). It is part of a band of subtropical humid forest that occurs semi-continuously in a northwest to southeast direction, especially on low mountains such as Volcán San Cristóbal, Rota, Masaya, and the volcanoes in Lake Nicaragua. More on the geology of this area can be found in Weyl (1980).

The significance of this geographic variant of *E. denarius* cannot be assessed at present. Its ventral wing pattern and genitalia are typical of *E.*

*denarius*. Of the 52 eumaeine species recorded from El Crucero/Las Nubes in Robbins et al. (2012a), *E. denarius* is the only one with a variant wing pattern. In the museum collections we examined, there are no individuals of *E. denarius* from other parts of this band of subtropical humid forest, so we cannot assess variation of the El Crucero/Las Nubes phenotype. In fact, the only other known Nicaraguan specimen of *E. denarius* is the type of *Thecla calena* from Chontales to the east of Lake Nicaragua (Robbins et al. 2012a). Finally, we note that some individuals from Mexico (Fig. 19) also have more dorsal orange suffusion than others, but not as much as those from El Crucero/Las Nubes.



## Species synonymies

Godman and Salvin (1887-1901: 77) synonymized *Thecla calena* with *Tmolus denarius*, but then described *Thecla plusios* writing “This is perhaps a doubtful species” because their specimens from Guatemala were in poor condition. In a checklist (Robbins 2004), these names were treated as synonyms. The wing pattern analysis in this paper confirms both synonymies.

Johnson (1992) described *Arases aurantiaca* from a male holotype. The verbal description of its male genitalia is nondescript. The referenced figure of the male genitalia was omitted. It is unclear whether the holotype (figured on the Butterflies of America web site ([www.butterfliesofamerica.com/L/Lycaenidae.htm](http://www.butterfliesofamerica.com/L/Lycaenidae.htm), accessed 19 May 2015) is male or female, based on its wing shape. Robbins (2004) synonymized this species with *E. guzanta*. Regardless of the sex of the holotype, the wing pattern analysis in this paper confirms the synonymy.

Johnson and Kroenlein (1993b) described *Kisutam simplis* from a female holotype and illustrated her genitalia along with those of *K. syllis* (Godman & Salvin). Comparing these stylized illustrations with those of *Kisutam* genitalia in Duarte and Robbins (2010) and Thompson and Robbins (2015), neither genitalia appears to belong to a species of *Kisutam*. In fact, so far as we are aware, neither would appear to be Calycopidina, unless these illustrations are inaccurate. According to the wing pattern analysis in this paper, the adult holotype female (figured on the Butterflies of America web site ([www.butterfliesofamerica.com/L/Lycaenidae.htm](http://www.butterfliesofamerica.com/L/Lycaenidae.htm), accessed 19 May 2015) is a female of *E. denarius*. Under Article 73.1.5 of the International Code of Zoological Nomenclature (ICZN 1999), we exclude the abdomen from the holotype, clarifying and confirming the synonymy of this species specific name with *E. denarius*, as proposed in Robbins (2004).

*Angulopsis strymonotis* Johnson & Kroenlein was described from a chimeric holotype. The holotype of *A. strymonotis* is described as “male” on p. 20 of the text, but the adult illustrated on figure 13 on plate 5 and its legend (on an unnumbered page) label it as “female”. The specimen in the BMNH labelled as holotype lacks a head and an abdomen and is identical to Johnson’s figure 13. It is illustrated on the Butterflies of America web site (<http://www.butterfliesofamerica.com/L/Lycaenidae.htm>, accessed 19 May 2015). The ventral wing pattern of the holotype of *A. strymonotis* is indistinguishable from syntypes of *E. joya* (Dognin) in the BMNH and USNM. The genitalia of the holotype of *A. strymonotis* is described as “male” on page 20 of the text, and figure 2F partially illustrates a male genitalia that appears to belong to the *E. guzanta* species complex.

Further, the original description of *A. strymonotis* states that brush organs about the male genitalia vinculum. Brush organs are present in the *E. guzanta* species complex, but are lacking in *E. joya* (Duarte & Robbins 2010). It would appear that the adult wings and abdomen of the holotype of *A. strymonotis* belong to different sexes and to different species, a chronically occurring problem with Johnson holotypes (cf. Robbins & Lamas 2002). Regardless, under Article 73.1.5 of the International Code of Zoological Nomenclature (ICZN 1999), we exclude the abdomen from the holotype. Consequently, *Angulopsis strymonotis* Johnson & Kroenlein, 1993 is a **new synonym** of *Electrostrymon joya* (Dognin, 1895), and the previous synonymy of *A. strymonotis* with *E. perisus* in a checklist (Robbins 2004), which was based on the genitalia, is now invalid.

## Nomenclatural list

The following classification of the *E. guzanta* species complex is based on the results of the qualitative and quantitative wing pattern analyses in this paper and various nomenclatural issues addressed above. In addition, the nomenclatural status of *Angulopsis strymonotis* is now changed so that it is a synonym of *E. joya*.

*Electrostrymon guzanta* (Schaus, 1902) (*Thecla*), type locality: Mexico (VER)

*aurantiaca* (K. Johnson, 1992) (*Arases*), type locality: Mexico (CHIA)

*Electrostrymon thurman* Thompson & Robbins, **new species**, type locality: Panama

*Electrostrymon perisus* (H.H. Druce, 1907) (*Thecla*), type locality: Venezuela

*Electrostrymon denarius* (Butler & H. Druce, 1872) (*Tmolus*), type locality: Costa Rica

*renarius* (Butler, 1873) (*Tmolus*), missp.

*calena* (Hewitson, 1877) (*Thecla*), type locality: Nicaragua

*plusios* (Godman & Salvin, 1887) (*Thecla*), type locality: Mexico (VER)

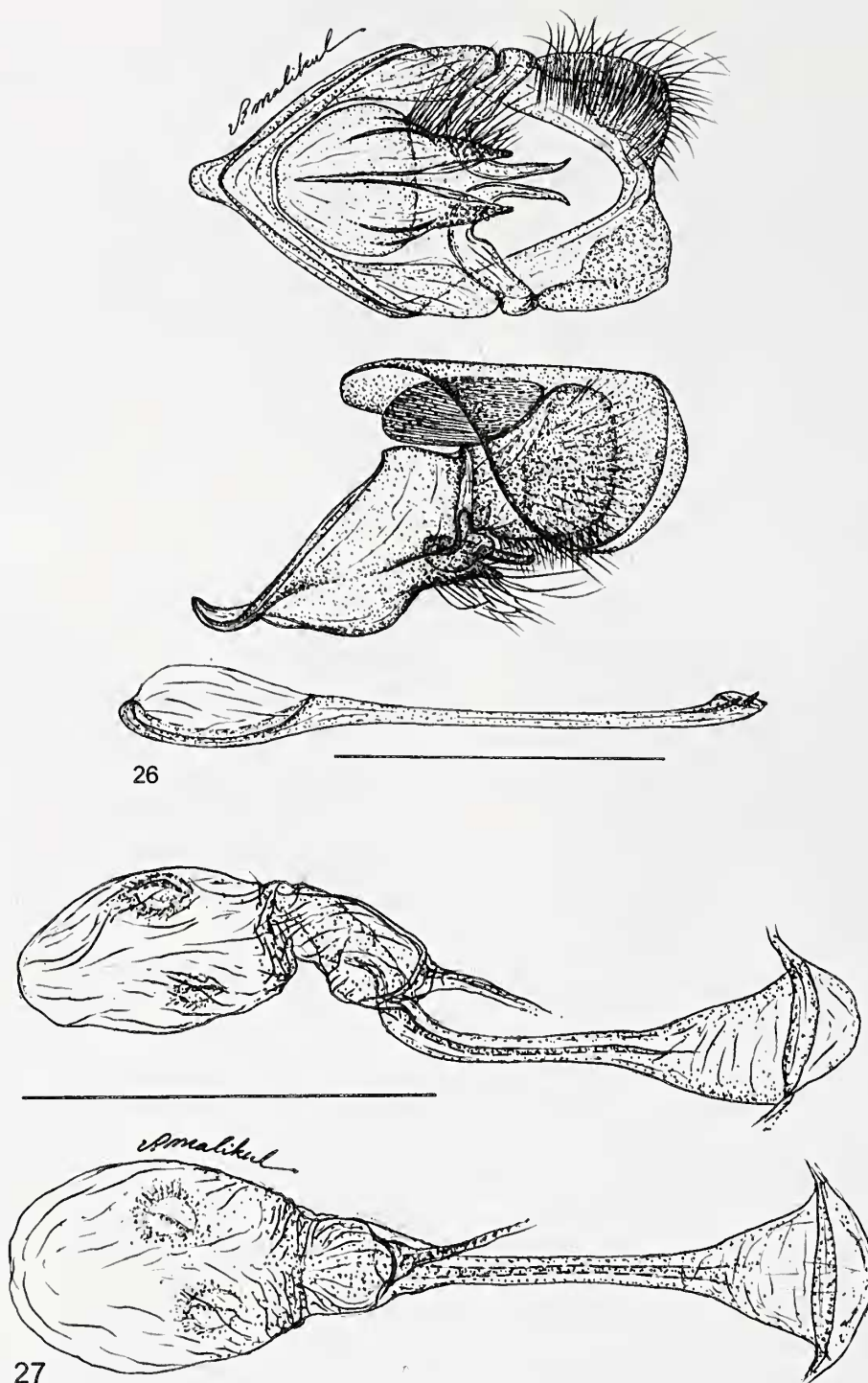
*simplis* (K. Johnson & Kroenlein, 1993) (*Kisutam*), type locality: Costa Rica, chimeric **holotype restricted** (ICZN, Art. 73.1.5)

*Electrostrymon joya* (Dognin, 1895) (*Thecla*), type locality: Ecuador

*strymonotis* (K. Johnson & Kroenlein, 1993) (*Angulopsis*), type locality: Ecuador, chimeric female **holotype restricted** (ICZN, Art. 73.1.5), **new synonym**

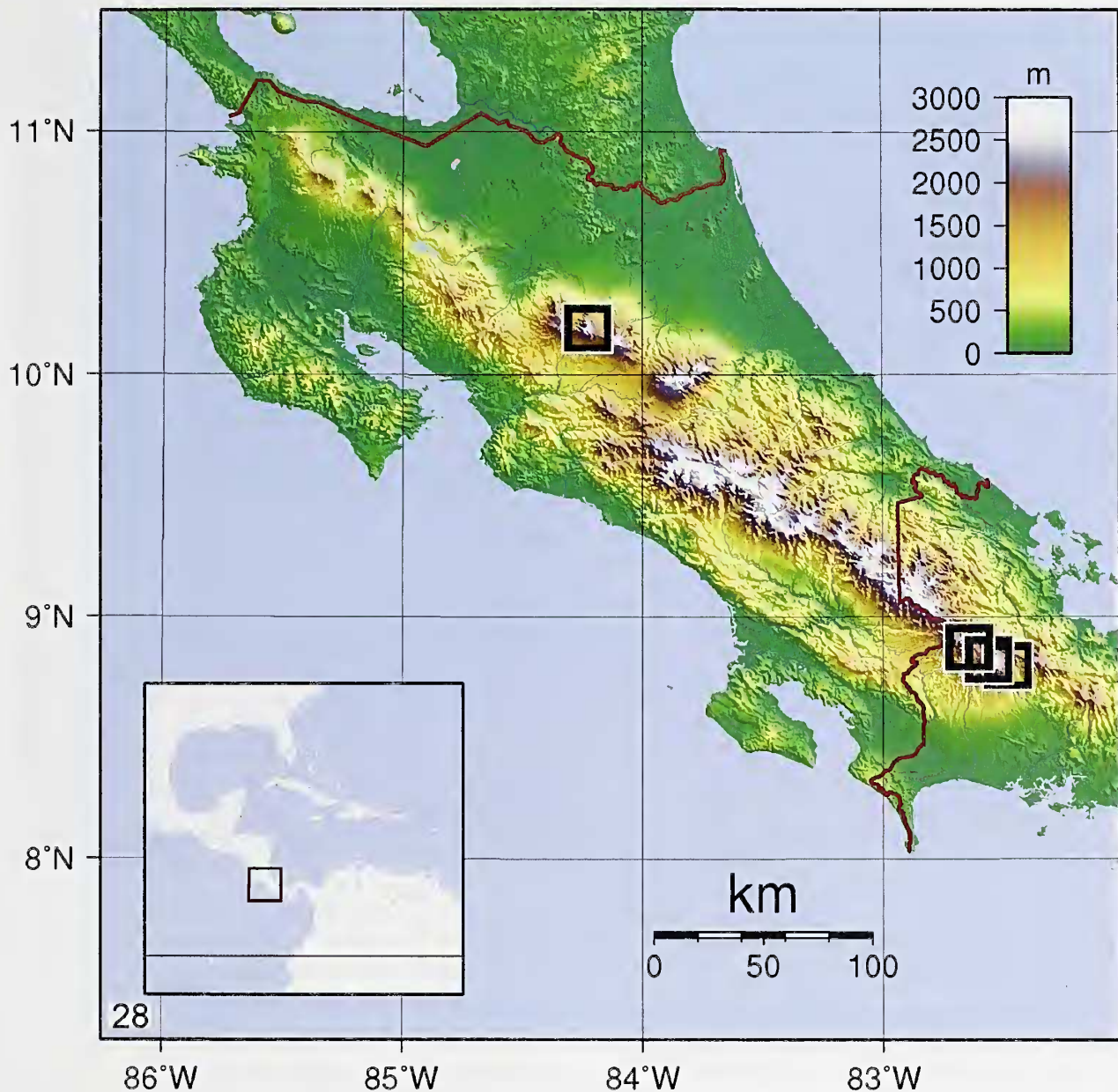
## Distribution and elevation

*Electrostrymon guzanta*, *E. thurman*, and *E. perisus* are allopatric. *Electrostrymon guzanta* is recorded from Mexico, Guatemala, El Salvador, and Nicaragua (records from the lowlands of the United States in Texas



**Figures 26-27.** Genitalia of *E. thurman*, posterior of insect to the right. 26. Male, ventral aspect (top), lateral aspect with 8<sup>th</sup> tergum (middle), and penis in lateral aspect (bottom). 27. Female, lateral (top) and dorsal aspects. Scale 1 mm.





**Figure 28.** Distribution of *E. thurman*.

are being addressed elsewhere); *E. thurman* from Costa Rica and Panama; and *E. perisus* from Venezuela and northern Colombia. The localities where *E. guzanta*, *E. thurman*, and *E. perisus* occur have elevations that range from 1,350 m to 2,550 m (Fig. 30). There are no statistical differences in mean locality elevation rank in pairwise comparisons among these three species (Table 3). *Electrostrymon guzanta* and *E. thurman* are separated by a gap of lowland habitat in southeastern Nicaragua, and *E. thurman* and *E. perisus* are similarly separated by the lowland Isthmus of Panama. There is

no evidence suggesting current dispersal across either of these lowland gaps.

The geographically most widespread species in the *E. guzanta* species complex is *E. denarius*, which is recorded from Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. Although the southeastern-most specimen of *E. denarius* was found near the Panama-Colombia border, this species is unrecorded from South America. The localities where *E. denarius* occurs have elevations that range from 50 to 1,750 m (Fig. 31). There are no statistical differences in





**Figure 29.** Cerro Totuma, Chiriquí, Panama (1,950 m elevation). Adult males and females of *E. thurman* were feeding on flowering trees at the edge of this ridgetop pasture.

mean locality elevation rank in pairwise comparisons of *E. denarius* in different countries (Table 3).

*Electrostrymon denarius* occurs at significantly lower elevations than the remainder of the species complex despite elevational overlap from 1,350 to 1,750 m (Fig. 32). The mean locality elevation rank for *E. denarius* in Mexico is significantly lower than that for *E. guzanta* ( $p < 0.05$ , Table 3). The mean locality elevation rank for *E. denarius* in Costa Rica and Panama is significantly lower than that for *E. thurman* ( $p < 0.05$ , Table 3). We could not compare *E. denarius* elevations with those of *E. perisus* because the former is unrecorded in South America.

#### Allopatry, parapatry, or sympatry?

The lack of male secondary sexual organs in Lepidoptera is associated with allopatry in closely related species (Phelan & Baker 1987, Robbins et al. 2012b). Genitalic differences are hypothesized to

result from sexual selection driven by female choice (Eberhard 2010, Simmons 2014), which then facilitates sympatry between closely related species following secondary contact. The four members of the *E. guzanta* species complex have uniform genitalia and lack wing secondary sexual structures. In accord with this theory, as already noted, *E. guzanta*, *E. thurman*, and *E. perisus* are allopatric with each other.

The elevational overlap between *E. denarius* and *E. guzanta*/*E. thurman* (Fig. 32) appears to falsify the predictions that these taxa should be allopatric or parapatric, but supplemental data would be needed to substantiate such a conclusion. Geographic range overlap is a characteristic of parapatric distributions due to reproductive interference (Key 1981, Bull 1991, Pettengill & Moeller 2012, Werner et al. 2014, Bournez et al. 2015). For example, adult insects can disperse to, and survive in, areas with reproductive interference, even if they do not successfully leave offspring.



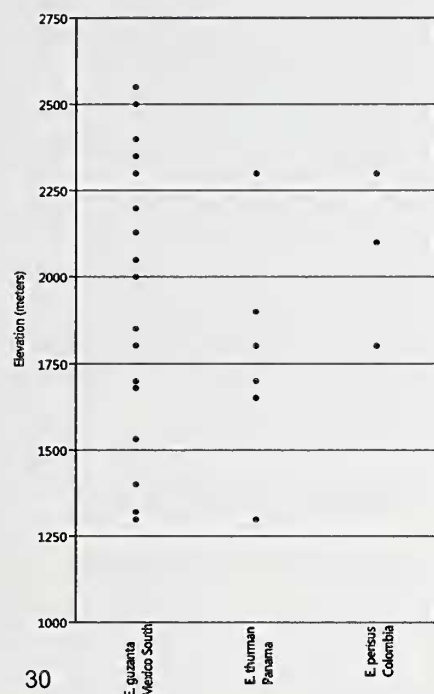


Figure 30. Locality elevations at which *E. guzanta*, *E. thurman*, and *E. perisus* have been found. There is no statistical difference among the species (Table 3).

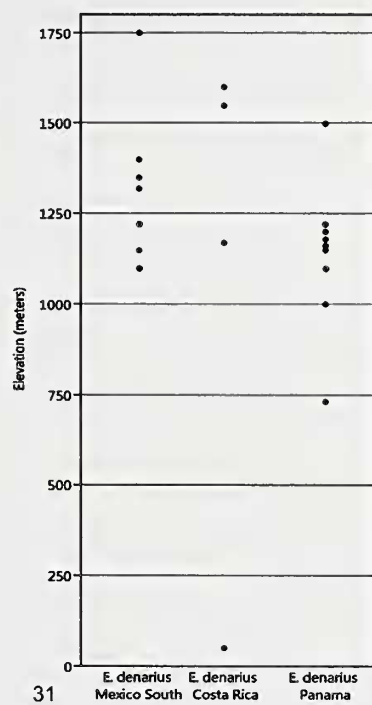


Figure 31. Locality elevations in different countries where *E. denarius* has been found. There is no statistical difference among the countries (Table 3).

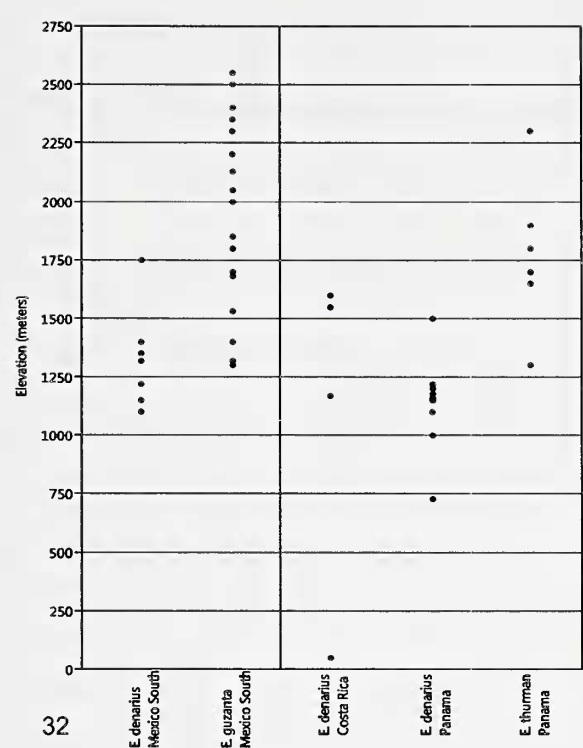


Figure 32. *Electrostrymon denarius* occurs at lower elevations than *E. guzanta* in Mexico and at lower elevations than *E. thurman* in Costa Rica/Panama (Table 3).

Documentation of reproductive biology is needed to determine whether the distributions of *E. denarius* and *E. guzanta*/*E. thurman* are parapatric, as predicted.

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### EDITOR'S NOTE

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank.org:pub:3F44721B-329C-4D14-BD8B-E8D11E8CBF1C. Registration date: 9 July 2016. This record can be viewed using any standard web browser by clicking on the LSID above.

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